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Modelling growth of blue shark (*Prionace glauca*) and silky shark (*Carcharhinus falciformis*) in the southwest Indian Ocean assessed by back-calculated length from vertebrae

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ABSTRACT

The blue shark (BSH), *Prionace glauca* and the silky shark (FAL), *Carcharhinus falciformis* are the main shark species taken as bycatch in the pelagic longline and purse seine fisheries in the Indian Ocean, respectively. Because of the paucity of the basic biological information and fishery statistics, population trends in the region cannot be assessed. Growth parameters are necessary for predicting population responses to fishing pressure but they remain unknown for these two populations. Growth parameters are crucial for both management and conservation purposes. Between 2009 and 2010, 188 BSH (36-276 cm LF) and 197 FAL (51-264 cm LF) were collected in the southwest Indian Ocean by observers and during scientific surveys. Of these samples, vertebrae were aged and distances between the centre of the vertebrae and each growth ring were determined to estimate back-calculated individual lengths at age. For both species, the relationship between fish length (L) and vertebrae radius (R) was best modelled by an allometric L-R model with a significant negative allometry for BSH (F-test, $P<0.001$) and a significant positive allometry for FAL (F-test, $P<0.05$). A NLME model based on the von Bertalanffy growth equation (VGBE) was fitted to back-calculated length data. Our results revealed that blue shark had a greater growth rate than FAL. Also, BSH and FAL reach a maximal asymptotic length (fork length, LF) of about 261 cm and 240 cm respectively for a maximum age ranged between 15 and 20 years. No sexual dimorphism on growth was detected. Growth parameter estimates for combined sexes of each population were: 0.89 ± 0.03 years for t_0 , $0.161 \pm 0.003 \text{ y}^{-1}$ for k , 258 ± 3 cm for LF_∞ for BSH and -2.38 ± 0.06 years for t_0 , $0.095 \pm 0.006 \text{ y}^{-1}$ for k , 230 ± 9 cm LF_∞ for FAL.

Keywords: Von Bertalanffy growth model | Purse seine fishery | Longline fishery | Stock assessment | NLME model

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1 INTRODUCTION

Most large pelagic sharks are apex predators controlling community structure and ecosystem processes (Cortès 2004; Lack and Sant 2011). This important functional groups is declining worldwide resulting from increasing shark catches (Holden 1974 [ENREF 41](#); Lack and Sant 2011), increasing by approximately 2 % per year (Camhi et al. 2007). A recent report indicates that shark captures in the Indian Ocean alone are approximately $198 \cdot 10^3$ metric tons (MT) annually (http://www.fao.org/figis/servlet/SQServlet?file=/work/FIGIS/prod/webapps/figis/temp/hqp_841488388365102158.xml&outtype=html).

Shark catches are commonly underestimated because of non-reported, under reported and illegal catches of pelagic sharks for their fins, for which there is a high demand in Asian markets. Moreover, sharks are often taken as bycatch of tuna fisheries, using longlines and gillnets (Morgan and Burgess 2007, Mandelman et al. 2008). Obtaining reliable assessments of the status of shark stocks is extremely difficult for species exploited as bycatch (Gilman et al., 2008). Sharks are predicted to be vulnerable to overexploitation because of their biological characteristics, such as late maturity, low reproductive output and being long-lived, predictions that are borne out by trends in historical elasmobranch fisheries. The removal of apex predators could initiate trophic cascades and have unanticipated impacts, such as modifying biogeochemical cycles or favoring invasive species (Cury and Miserey, 2012).

The blue shark, *Prionace glauca*, is a large pelagic carcharhinid with a circumglobal distribution. Throughout its range, it is considered as the most abundant species among large sharks. In the tropical Indian Ocean, blue shark occurs mostly at depths between 80-220 m where seawater temperatures range between 12-25 °C (Last and Stevens, 1994). The blue shark is primarily taken as bycatch in Indian Ocean longline fisheries and can be targeted by some pelagic longline fisheries (Lirdwitayaprasit et al. 2012). It represents 18.2% of the shark-fin trade in Hong Kong (Clarke et al. 2006). Catches of blue shark in the Indian Ocean have been estimated at 171 MT in 1986, at 595 MT in 1990, 9014 MT in 2000, and around 7767 MT in 2010 (FAO FIGIS, 2012). Most blue shark that is caught accidentally by pelagic longlines is discarded dead or released alive with ~19 % post release mortality (Campana et al. 2009). Cailliet and Bedford (1983) first detected sexual dimorphism in a blue shark population from the eastern Pacific, with males growing faster and attaining larger size than females. Lessa et al. (2004), who used back-calculation from growth rings in vertebrae

of males and females, did not detect sexual dimorphism in a *P. glauca* population from northeastern Brazil. Growth rate is intermediate in the Atlantic Ocean (Aasen 1966; Steven 1975; Silva et al. 1996; Henderson et al. 2001) and slow in the Pacific Ocean (Cailliet and Bedford 1983; Blanco-Parra et al. 2008).

The silky shark, *Carcharhinus falciformis*, is common in coastal warm temperate and tropical regions worldwide. They spent 85 % of their time in water with temperatures of 26–30 °C (Filmalter et al., 2011) and are found between 18-500 m depth. In recent years, silky shark abundance has declined drastically worldwide. It is targeted by coastal and offshore tropical fisheries (Oshitani et al. 2003), but is also one of major bycatch species of purse-seine tuna fisheries, generally discarded or fished by ghost nets under fish aggregating devices (Amandé et al., 2011, Filmalter et al., 2013). This species represents 3.5 % of the shark-fin trade in Hong Kong (Clarke et al. 2006). Filmater et al. (2013) reported annual captures of silky shark of 577 MT in the Indian Ocean but accurate information on catches is lacking. In consequence, the status of most silky shark stocks is poorly known, except for the Atlantic Ocean. Recently, Filmalter et al. (2013) reported on the alarmingly high mortality induced by Fish Aggregating devices (FAD) on Indian Ocean silky shark populations.

Information on life history traits of silky shark populations in the Pacific and Atlantic oceans has been summarized by Compagno (1984). Maximum size is over 300 cm LF and new born pups are ≤75-80 cm LT at birth. Branstetter (1987) first studied age and growth of combined sexes with maximum size around 250 cm LF, while Joung et al. (2008) first reported sexual dimorphism with females larger than males. Sanchez de Ita (2011), the first to use growth back-calculation, did not detect sexual dimorphism. Growth rate is slow (Joung et al. 2008) or intermediate (Branstetter 1987; Oshitani et al. 2001, Sanchez de Ita 2011).

Biological information on blue and silky sharks from the Indian Ocean is still very scarce. Both species fall both in the category of near threatened (NT) on the IUCN red list; the status of their stocks in the Indian Ocean has not yet been ascertained as shark catches are not recorded at species level (IUCN, 2013). In the southwest Indian Ocean (SWIO) basic knowledge on age and growth of *P. glauca* and *C. falciformis* is lacking, parameters that are essential for demographic population analyses. This study presents for the first time the length - age relationships and growth parameters of the blue shark and silky shark populations in the SWIO by using back-calculation of lengths corresponding to growth rings read from vertebrae.

2 MATERIAL & METHODS

2.1 Collection of the biological material

Individuals of *Carcharhinus falciformis* and *Prionace glauca* were collected in 2009 and 2010 during commercial longline fishing operations with an observer on board and during scientific longline fishing campaigns in the SWIO (Figure 1). For each individual, the fork length (LF),

sex and status at hauling (alive, exhausted, dead) were noted, as well as the reproductive status of females and the number of embryos if present. A section of vertebral column from the region next to the posterior gill slit was collected and stored frozen.

2.2 Growth rings identification and measures on vertebrae

Back-calculation of fish growth from calcified structures (i.e., otoliths, vertebrae, statoliths, scales) involves measurements made on these structures to infer body length at ages prior to capture. Growth rings on vertebrae are commonly used for shark age estimation (Campana, 2001). A growth ring (GR) is defined as a pair of opaque and translucent bands assumed to be formed annually by alternating slow growth in northeast monsoon and faster growth in southwest monsoon. Age was assigned according to the number of GR starting from the birth mark to the edge of the corpus calcareum of a sectioned vertebra (Figure 2). The birth mark was defined as the first GR nearby the vertebra centrum. Only the easily distinguished dark bands were counted without prior knowledge of the fish length.

In the laboratory, the vertebral column section was thawed, cleaned of excess tissue and separated into individual vertebra. One vertebra was selected haphazardly for analysis and dried in the sun or in a stove at 40 °C during 24 hours. A low-speed saw (Beuhler Isomet) equipped with two parallel diamond blades was used to obtain a 0.7-0.8 mm thick sagittal section of the vertebra. Sections were mounted on glass slides and examined under a binocular microscope with transmitted light at 7x - 11x magnification. Growth rings were photographed with a digital camera (Olympus ORCA 285) at 300 dpi resolution and analyzed using TNPC software (Fablet & Ogor 2007; <http://www.tnpc.fr/en/tnpc.html>). Poor contrast of the growth rings makes some vertebrae difficult to read. Brightness and contrast of images of vertebral growth ring were enhanced using Adobe Photoshop and aged twice in blind manner by the same observer (N.R.) at 2-month intervals. Age estimates may therefore be biased and vertebrae with a minimum difference of three growth rings between two age readings were removed from the analysis.

2.3 Back-calculation of size-at-age

The radius of the vertebra was measured along a straight line from the focus to the most distal edge of the corpus calcareum. Subsequently, the radius (R) of each GR (dark band) was measured. Back-calculation of fish growth from GRs in calcified structures has been reviewed by Vigliola and Meekan (2009). These authors recommended using the modified Fry back-calculation model (eq. 1) as most fish display either a linear (eq. 2) or an allometric (eq. 3) relationship between the radius R of calcified structures and length L :

$$L_i = a + \exp \left\{ (\ln(L_{op}) - a) + [\ln(L_{Cpt}) - a] - \ln(R_{op} - a) + \frac{[\ln(R_i) - \ln(R_{op})]\gamma}{[\ln(R_{Cpt}) - \ln(R_{op})]} \right\} \quad \text{eq. 1}$$

$$L_{Cpt} = L_{op} - bR_{op} + bR_{Cpt} \quad \text{eq. 2}$$

$$L_{Cpt} = L_{op} - bR_{ip}^{\alpha} + bR_{Cpt}^{\alpha} \quad \text{eq. 3}$$

where L_i is fish length at age i , L_{0p} is fish length at biological intercept, L_{cpt} is fish length at capture, R_i is radius of calcified structure at age i , R_{0p} is radius of calcified structure at biological intercept, R_{cpt} is radius of calcified structure at capture, and a is theoretical fish length at calcified structure formation, c allometry coefficient.

Following these authors, we used shark vertebrae radius in growth back-calculations using equation 1. For both species we assumed that the first increment corresponded to the birth mark in vertebrae. Equations 2 and 3 were fitted by non linear regression in order to evaluate the shape (linear/isometric or curvilinear/allometric) of the relationship between fish length and vertebrae radius, and to estimate a . Vigliola and Meekan (2009) indicated that $a = L_{cp} - bR_{0p}$ if c was not significantly different from 1 (isometry/linear shape) in eq. 3 and $a = L_{cp} - bR_{0p}^c$ if c was significantly different from 1 (curvilinear/allometry) in eq. 3.

2.4 Adjustment of the growth model

Cailliet et al. (2006) reviewing elasmobranch age and growth studies recommended the use of the von Bertalanffy growth function (VBGF) based on two parameters by fixing the L_0 parameter as the empirical size at birth. While this approach aims to save of degree of freedom in the model fitting process, a recent studies (Pardo et al., 2013) strongly recommended to use the three-parameter VBGF. Moreover, data generated from growth back-calculations are longitudinal and auto-correlated and these properties must be taken into account for statistical purposes. The use of a non-linear mixed-effect model (NLME) framework has been recommended in such cases. Growth trajectories of both shark species were modeled by a standard von Bertalanffy growth function (VBGF; eq. 4); fitted using NLME:

$$L_{Ft} = L_{F\infty} [1 - \exp(-K(t - t_0))] \quad \text{eq. 4}$$

where L_{Ft} is the fork length (cm) at age t (in years, y), $L_{F\infty}$ is the asymptotic fork length, K is instantaneous growth (y^{-1}), and t_0 is the predicted age when individuals have a length of zero. For each species, sex was included as a factor in the NLME in order to test for differences in growth parameters (t_0 , L_∞ , and K) between sexes. NLME models were fitted using the Fisher maximum likelihood estimates and best fits selected using the Akaike Information criterion (AIC). Longevity was calculated from the empirical relationship of Skomal and Natanson (2003):

$$T(0.99) = 5 + \frac{\ln 2}{K}$$

3 Results

3.1 Size, age and sex of shark individuals analyzed

Sampled *Prionace glauca* ($n = 188$) ranged between 36-276 cm LF with mean size (\pm SD) of 185 ± 39 cm LF (Figure 3A). Estimated ages of the total sample ranged from 1-15 y with a mean of 7 ± 3 y. Mean size of sexually mature females ($n = 93$) was 187 ± 34 cm LF (min/max = 90/260 cm) and of males ($n = 89$) 189 ± 32 cm LF (min/max = 110/276 cm) (Figure 3A). Ages ranged between 1-14 y for females (mean: 8 ± 3 y) and from 2-15 y for males (mean: 8 ± 3 y). 50% estimated size at maturity is 150 cm LF, therefore the *P. glauca* samples predominantly consisted of subadult and adult individuals. One female of 243 cm LF contained four embryos ranging from 36-38 cm LF.

Mean size of *Carcharhinus falciformis* individuals considered in this study samples ($n = 197$) was 97 ± 29 cm and ranged between 51-264 cm LF (Figure 3B). Estimated ages for this species ranged from 0-16 y with a mean age of 3 ± 2 y. Females ($n = 100$) had a mean size of 98 ± 32 cm LF (min/max = 53/264 cm) and males ($n = 97$) a mean size of 96 ± 26 cm LF (min/max = 51/197 cm) (Figure 3B). Estimated age of female *C. falciformis* ranged from 0-16 y, but was low on average (3 ± 2 y). Age of males ranged from 0-9 y, with similar low mean age (3 ± 2 y). 50% estimated size at maturity was cm 144 cm LF. Thus, the *C. falciformis* sample was dominated by immature individuals (91 cm), with few adults.

3.2 Growth modelling

The relationship L (length of fish) – R (vertebrae radius) could be allometric at the level of individuals but linear at the level of the population. Indeed, back-calculation based on an allometric model gave more precise size-at-age estimates than that based on a linear model, even when the relation L-R is linear at the population level (Vigliola and Meekan, 2009).

For both species, the relationship between fork length (LF) and vertebrae radius (R) was better statistically described by an allometric relationship (eq. 3), with a significant negative allometry for *P. glauca* (F-test, $P < 0.001$) and a significant positive allometry for *C. falciformis* (F-test, $P < 0.05$) (Table I), Figure 4.

Blue and silky sharks have respectively an average length at birth $L_{0p} = 34.71$ cm LF and $L_{0p} = 47.73$ cm LF_F, and an average vertebrae radius at first increment $R_{0p} = 1.95$ cm for *P. glauca* ($n = 188$) and 1.94 cm for *C. falciformis* ($n = 197$).

NLME model fits of the VBGF revealed that both shark species had a relatively slow growth, attaining a maximum size of about 200-250 cm LF for an age range of 15-20 years (Figure 5). Models indicated that none of the VBGF parameters significantly differed among males and females and log-likelihood ratio tests were resumed in Table I. For both species, individual growth trajectories formed a relatively homogeneous envelope around the

population growth trajectories (Figure 5). Longevity is 22 years for blue shark and 26 years for silky shark.

4 Discussion

4.1 Back Calculation

The principle of growth back calculation is to infer fish size-at-age from the measurement of increments on hard structures, vertebrae for sharks. Because each individual has a unique morphology (some with big vertebra with regard to their size, and others with small vertebra), some dispersion is typically observed in the relationship between the length of the fish and the radius of the hard structure. This was particularly visible here for the blue shark. Back-calculation and NLME allow accounting for this individual variability. Misinterpretation of the vertebrae ageing affected result of back calculation. We must bear in mind that results obtained from back-calculation also strongly depend on the choice of model. The few studies that have tested different back-calculation models reported relatively similar growth parameters, suggesting that growth estimates are relatively robust with regards to model choice (see Vigliola and Meekan 2009 for a review). Here, we used the modified Fry's back-calculation model recommended in the case where a validation of back-calculation models was not possible, which is the case for the present study.

4.2 Growth parameters

Blue shark

The K value for blue shark reported here from the Indian Ocean (0.16 ± 0.003) is higher than values from Pacific populations but very similar to that estimated for a population from the western Atlantic (Table II). We found asymptotic length to be larger than reported in one study from the Pacific (Cailliet and Bedford, 1983) but smaller than most other values for *P. glauca* from all oceans, (Lessa et al., 2004, Blanco-Parra et al. 2008, Silva et al., 1996). Indeed, the infinite length estimated from back-calculated length-at-age corroborate with the maximal lengths recorded in the Indian Ocean.

Atlantic and Indian Ocean populations show intermediate growth rates whereas blue sharks from the Pacific grow more slowly (Table II). However, maximum age of Indian Ocean blue shark was older than that obtained for similar-sized blue sharks from the Atlantic (>15 years vs. 11 years respectively). Size at birth obtained in this study is among the smallest recorded. The calculated size at birth of 33.8 cm LF corresponded to the lower value of the size range at birth of 35–44 cm LF reported in the Indian Ocean (IOTC, 2007). However, Joung et al. (2004) mentioned that size at birth (L_0) estimated by VBGF is less than the size of full-term embryos when estimated by simple regression.

Silky shark

The studied Indian Ocean population of silky shark exhibits a slow growth rate ($K = 0.09$, for both sexes combined), contrasting with the intermediate growth values obtained from the Atlantic and Pacific Oceans even if sampling is debatable. Moreover, size at birth, at sexual maturity and asymptotic size in this study are among the smallest of all oceans (Table II).

The size of the smallest and largest specimens in the samples do affect the estimation of fish growth parameters. Most of silky shark's sample corresponded to young individuals and a few subadults, while large specimens were underrepresented. This result is likely a consequence of the size selectivity of fishing gears (purse seine and pelagic longline) used to collect our data. Purse seiners captured only juvenile silky sharks abounding inshore under floated objects (Amandé et al., 2010). Longliners were more active offshore covering the horizontal habitat of adult silky sharks. However, high $\delta^{15}\text{N}$ values of silky sharks caught by longliners reflect their foraging on prey at great depths (Rabehagasoa et al., 2012) not accessible to the gear deployed at surface to target swordfish during nighttime. Alternatively, the lack of large-bodied individuals in our sample may reflect a decrease of the population due to the high fishing pressure.

The back calculated size at birth (44.3 cm LF) is substantially less than pup's size of 61-66 cm LF recorded in the Indian Ocean (IOTC, 2007). Back calculated size at birth coincided with average size at birth in Maldivian waters (46-52 cm LF) but is smaller (59-66 cm LF) than in the Pacific (Bonfil et al. 2008, Joung et al. 2008, Oshitani et al. 2001).

Discrepancies in growth parameters among studies either for blue or silky sharks may be genetically determined and/or due to environmental factors or due to the history of the fishing pressure that can lead to a shift of some life history traits parameters (Sharp and Hendry 2009). Geographical differences in growth parameters among areas have been documented for some shark species. Methodological differences have also been invoked to explain differences in growth rates among studies for same species. Unlike in several other studies, we did not stain vertebrae before readings. Experience of readers on growth marks and the staining technique may have affected ageing and thus growth estimates. However, it is impossible to conclude whether the differences in growth parameters reported by different studies are due to sampling bias or realistically reflect population/environmental differences. Faster growth of *P. glauca* in the Indian and Atlantic Oceans than in the Pacific may reflect differences in oceanic productivity.

4.3 Sexual dimorphism and sexual maturity

Blue shark

For *P. glauca*, no sexual difference in growth parameters was detected in present study. Previous studies found males in the Pacific to be larger and males in the Atlantic to be smaller than females (Table II). And yet, males in the Pacific grow slowly while in the Atlantic they display a slightly faster growth rate than females. Mean asymptotic length of *P. glauca* (255 cm LF in this study) for combined sexes is lower than values reported elsewhere. For

instance, Gubanov and Grigoryev (1975) reported males of 288 cm LF and females of 279 cm LF from the Indian Ocean. Moreover, males are consistently reported to be larger than females. This concurs with Compagno's (1984) results, reporting that blue shark males and females reach similar maximum sizes.

Size at the sexual maturity (50% of mature individuals) corresponding to the age of 5 years is estimated at 150 cm LF. In the Atlantic Ocean, sexual maturity occurred at 183 cm LF for both male and female (Skomal and Natanson, 2003; Silva et al. 1996). In the Pacific Ocean, females were smaller at maturity than males (Blanco-Parra et al. 2008; Tanaka et al., 1990; Nakano 1994) except for Cailliet and Bedford (1983) who found similar size at maturity for the two sexes.

Silky shark

In the present study, no sexual difference in growth parameters of *C. falciformis*, was detected. The same observation was made by Oshitani et al. (2001) in the Pacific but Joung et al. (2008) found that females grow more slowly but have bigger asymptotic size than males. Back calculated size at birth in this study is similar (50 cm LF) for both sexes. Back calculation with silky shark in this study indicated that sexual maturity corresponding to age of 8 years (50% of mature individuals) occurred at 144 cm LF and growth parameters did not differ between male and female. For the two species, the existence of many stocks of blue and silky sharks may induce variations of the size at first sexual maturity, growth rate and size for a given age between individuals and areas. Differences in sizes between sexes may be explained by the reduced growth rate after sexual maturity. The occurrence of sexual differences in growth is well documented in elasmobranch even if no sexual dimorphism was detected for the two populations considered. Gear selectivity and fishing area may contribute to the absence of sexual dimorphism because the unbalanced status of our samples.

4.4 Data on life history traits and management

As most shark species, blue and silky sharks in this study are long-lived (15-20 years), have late sexual maturity and limited offspring. The 'shark' component of pelagic ecosystems suffers from a cruel lack of accurate capture data that precludes any quantitative approach of stock and ecosystem management (Worm et al. 2013).

In order to be able to supply recommendations and management in this kind of situation called "data-limited" or "data-poor" expert developed the ecological risk assessment "ERA" approach (Hobday et al., 2011) and specifically the Productivity and Susceptibility Analysis (PSA). In this framework, the Productivity and Susceptibility Analysis (PSA) provides graphically scores on an x-y for a scatter plot to discriminate between species with a high productivity and a low susceptibility considered little vulnerable (low risk) and species with low productivity and high susceptibility considered highly vulnerable (high risk). The vulnerability corresponds to a measure of the resilience of the species to the impact of the fishery (Cortés et al., 2010).

Recently, a PSA was undertaken for pelagic sharks in the Indian Ocean (Murua et al., 2012). For blue shark and silky shark, growth parameters selected were those observed for the Atlantic Ocean ($K=0.15$, $L_{\infty}=375$ cm, $t_0=-0.87$, $L_{mat}=219.5$) and for the Indian Ocean ($K=0.057$, $L_{\infty}=320.4$ cm, $L_0=81.1$ cm, $L_{mat}=168.7$), respectively. In this study, growth parameters are ($K=0.16\pm0.003$, $L_{\infty}=258\pm3$ cm, $t_0=-0.89\pm0.03$, $L_{mat}=157.4$) for the blue shark and ($K=0.095\pm0.006$, $L_{\infty}=230\pm9$ cm, $t_0=-2.38\pm0.06$, $L_{mat}=144.2$) for silky shark. By comparing our values to those used by Murua et al. (2012) productivity estimates might change. In the case of blue shark, differences observed in L_{∞} , the maximum age and the length at maturity are those that might cause a large difference in the productivity which would be higher. For the silky shark, the same parameters are concerned even if L_{mat} values are more similar in that case. As for blue shark, these differences might lead in a productivity much higher. Then for these two species the vulnerability to fishing pressure would be lower than previously estimated. However, this hypothesis must be considered cautiously as the productivity is sensitive to others important parameters such as the total mortality which could be estimated from catch curves, the fecundity and the reproductive cycle duration. For all of them, more research must be undertaken.

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6 REFERENCES

- Amandè, M. J., J. Ariz, et al. (2011). Bycatch and discards of the European purse seine tuna fishery in the Atlantic Ocean: estimation and characteristics for 2008 and 2009. Collect. Vol. Sci. Pap. ICCAT, SCRS/2010/141 66(5): 2113-2120.
- Amorim, A. F. (1992). Estudo da pesca e reprodução do cação-azul *Prionace glauca* L. 1758, capturado no Sudeste e Sul do Brasil. D.Sc. Thesis. Universidade Estadual Paulista, Rio Claro: 205pp.
- Anderson, R. C. and H. Ahmed (1993). Shark fisheries of Maldives. Ministry of Fisheries and Agriculture. Maldives and FAO, Rome.

- Beerkircher, L., M. Shivji, et al. (2003). A Monte Carlo demographic analysis of silky shark (*Carcharhinus falciformis*): implications of gear selectivity. *Fishery Bulletin* 101: 168-174.
- Blanco-Parra, M. d. P., F. Galván-Magaña, et al. (2008). Age and growth of the blue shark, *Prionace glauca* Linnaeus, 1758, in the Northwest coast off Mexico. *Revista de Biología Marina y Oceanografía* 43(3): 513-520.
- Bonfil, R. (2003). Consultancy on elasmobranch identification and stock assessment in the Red Sea and Gulf of Aden. Final Report presented to the Regional Organization for the Conservation of the Environment of the Red Sea and Gulf of Aden, Jeddah: 195 pp.
- Bonfil, R., R. Mena, et al. (1993). Biological parameters of commercially exploited silky sharks, *Carcharhinus falciformis*, from the Campeche Bank, Mexico. NOAA Tech. Rep. NMFS 115: 73-86.
- Branstetter, S. (1987). Age, growth, and reproductive biology of the silky shark, *Carcharhinus falciformis*, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. *Environmental Biology of Fishes* 19: 161-173.
- Cailliet, G. and K. Goldman (2004). Age determination and validation in chondrichthyan fishes. In: Carrier J, Musick JA, Heithaus MR (eds), *Biology of sharks and their relatives*. CRC Press LLC, Boca Raton, Florida,: 399-447.
- Cailliet, G. M. and D. W. Bedford (1983). The biology of three pelagic sharks from California waters, and their emerging fisheries: a review. *CalCOFI Report* 24: 57-69.
- Cailliet, G. M., W. D. Smith, et al. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* 77: 211-228.
- Campana, S. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J Fish Biol* 59: 197-242.
- Campana, S. E., A. Dorey, et al. (2011). Migration Pathways, Behavioural Thermoregulation and Overwintering Grounds of Blue Sharks in the Northwest Atlantic. *Plos One* 6(2): 1-13.
- Campana, S. E., W. Joyce, et al. (2009). Bycatch and discard mortality in commercially caught blue sharks *Prionace glauca* assessed using archival satellite pop-up tags. *Mar Ecol Prog Ser* 387: 241-253.
- Campana, S. E., L. J. Natanson, et al. (2002). Bomb dating and age determination of large pelagic sharks. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 450-455.
- Carlson, J. K. and J. R. Sulikowski (2006). Do differences in life history exist for blacktip sharks, *Carcharhinus limbatus*, from the United States South Atlantic Bight and Eastern Gulf of Mexico? *Environmental Biology of Fishes* 77: 279-292.
- Castro, J. A. and J. Mejuto (1995). Reproductive parameters of blue shark *Prionace glauca* and other sharks in the Gulf of Guinea. *Marine and Freshwater Research* 46: 967-973.
- Chambers, R. C. and T. J. Miller. (1995). Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. In, *Recent developments in fish otolith research*. D. H. Secor, J. M. Dean, and S. E. Campana, editors. University of South Carolina Press, Columbia, SC 764: 155-175.

- Clarke, S. C., J. E. Magnusson, et al. (2004). Identification of Shark Species Composition and Proportion in the Hong Kong Shark Fin Market Based on Molecular Genetics and Trade Records. *Conservation Biology* 20(1): 201-211.
- Clarke, S. C., J. E. Magnusson, et al. (2006). Identification of shark species composition and proportion in the Hong Kong shark fin market based on molecular genetics and trade records. *Conservation Biology* 20 (1): 201-211.
- Compagno, L. (2001). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fishery Purposes 2 (1): 269 pp.
- Compagno, L. J. V. (1984). Sharks of the World: An Annotated and Illustrated Catalogue of Shark Species Known to Date. FAO Species Catalogue: Vol. 4, Part 2 Sharks of the world, FAO Fisheries Synopsis No. 125, 655 pp).
- Cortés, E. (2002). Catches and catch rate of pelagic sharks from the northwestern Atlantic, Gulf of Mexico and Caribbean. *Col. Vol. Sci. Pap. ICCAT* 54 (4): 1164-1181.
- Cortés, E. (2004). Life history patterns, demography, and population dynamics. Chapter 15 (pp. 449-469) In: (J.C. Carrier, J.A. Musick, and M.R. Heithaus, ed s.) *Biology of Sharks and Their Relatives* (CRC Press).
- Cortès, E. (1999). Standardized diet compositions and trophic levels of sharks. *ICES Journal of Marine Science* 56: 707-717.
- Dragonik, B. and W. Pelzarski (1983). The occurrence of the blue shark, *Prionace glauca* (L.), in the North Atlantic. *Rep. Sea Fish. Inst* 19: 63-77.
- Driggers, W., J. Carlson, et al. (2004). Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. *Environmental Biology of Fishes* 71: 171-178.
- Dulvy, N. K., Baum, C. J.K., et al. (2008). Global status of oceanic pelagic sharks and rays.
- Estes, J. A., J. Terborgh, et al. (2011). Trophic Downgrading of Planet Earth. *Science* 333(301).
- Fablet, R. and A. T. Ogor (2007). TNPC: digital processing of calcified structures. http://www.ifremer.fr/lasaa/TNPC/manuel_tnpc4_en.
- FAO (2011). Fishery Statistical Collections: Global Production. <http://www.fao.org/fishery/statistics/global-production/query/en>.
- Ferreira, B. P. and C. M. Vooren (1991). Age, growth, and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. *Fishery bulletin* 89: 19-31.
- Filmalter J., F. Forget, F. Poisson, A.-L. Vernet, P. Bach and L. Dagorn, 2012 - Vertical and horizontal behaviour of silky, oceanic whitetip and blue sharks in the western Indian Ocean. IOTC–2012–WPEB08–23.
- Francis, M. P., L. H. Griggs, et al. (2001). Pelagic shark bycatch in the New Zealand tuna longline fishery. *Mar. Freshwater Res.* 52(2): 165–178.

- Gillman, E.L. (2011). Bycatch governance and best practice mitigation technology in global tuna fisheries. Mar. Policy 35: 590-609
- Gruber, S. H. (2000). Life style of sharks. Shark Conference 2000, Online Documents, Honolulu, Hawaii February 21-24
- Hazin, F. H. V. (1991). Ecology of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic. M.Sc. Dissertation. Tokio University of Fisheries: 123 pp.
- Hazin, F. H. V., P. G. V. Oliveira, et al. (2007). Aspects of the reproductive biology of silky shark, *Carcharhinus falciformis* (Nardo, 1827), in the vicinity of Archipelago of Saint Peter and Saint Paul, in the equatorial Atlantic Ocean. Col. Vol. Sci. Pap. ICCAT, SCRS/2006/176 60(2): 648-651.
- Heithaus, M. R., A. Frid, et al. (2008). Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 23 (4): 202-210.
- Henderson, A. C., K. Flannery, et al. (2001). Observations on the biology and ecology of the blue shark in the North-east Atlantic. Journal of Fish Biology 58: 1347-1358.
- Holden, M. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In: Jones EH (ed) Sea fisheries research. Logos, London: 187-215.
- Holden, M. J. (1977). "Elasmobranchs." In: Gulland, J.A. (Ed.), Fish Population Dynamics. John Logos, London: 187-214.
- IOTC (2010). Executive summary of the status of the blue shark resource. IOTC-2010-SC-06a.
- Joung, S.-J., C.-T. Chenb, et al. (2008). Age, growth, and reproduction of silky sharks, *Carcharhinus falciformis*, in northeastern Taiwan waters. Fisheries Research 90: 78-85.
- Kitchell, J. F., T. E. Essington, et al. (2002). The Role of Sharks and Longline Fisheries in a Pelagic Ecosystem of the Central Pacific. Ecosystems 5: 202-216.
- Lack, M., and Sant, G. (2011). The future of sharks: a review of action and inaction. TRAFFIC International and the Pew Environment Group.
- Lessa, R., F. M. Santana, et al. (2004). Age and growth of the blue shark *Prionace glauca* (Linnaeus, 1758) off northeastern Brazil. Fisheries Research 66 19-30.
- Lombardi-Carlson, L., E. Cortés, et al. (2003). Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. Marine and Freshwater Research 54: 875-883.
- Manning, M. J. and M. P. Francis (2005). Age and growth of blue shark (*Prionace glauca*) from the New Zealand Exclusive Economic Zone. New Zealand Fisheries Assessment Report 2005/2006.
- McCosker, J. E. (2008). Sharks of the Open Ocean: Biology, Fisheries and Conservation. Fish and Fisheries: 502pp.
- McKenzie, R. A. and S. N. Tibbo (1964). A morphometric description of the blue shark (*Prionace glauca*) from the Canadian Atlantic waters. J. Fish. Res. Board Can. 21: 865-866.

- Murua H., R. Cohelo, M.N. Neves, H. Arrizabalaga, K. Yokawa, E. Romanov, J.F. Zhu, Z.G. Kim, P. Bach, P. Chavance, A. Delgado de Molina and J. Ruiz, 2012 - Preliminary Ecological Risk Assessment (ERA) for shark species caught in fisheries managed by the Indian Ocean Tuna Commission (IOTC). IOTC-2012-WPEB08-31 Rev_2.
- Nakano, H. (1994). Age, reproduction and migration of blue shark in the North Pacific Ocean. Bulletin of the National Research Institute of Far Seas Fisheries Enyosuikenho 31: 141-256.
- Natanson, L., J. Casey, et al. (1995). Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fishery Bulletin 93: 116-126.
- Natanson, L. J., J. J. Mello, et al. (2002). Validated age and growth of the porbeagle shark (*Lamna nasus*) in the western North Atlantic Ocean. Fishery Bulletin 100: 266-278.
- Oshitani, S., H. Nakano, et al. (2003). Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean." Fisheries science 69: 456-464.
- Parker, H. W. and F. C. Scott (1965). Age, size and vertebral calcification in the basking shark, *Cetorhinus maximus* (*Gunnerus*). Zoologische Mededelingen Museum Natuurlijke Historie, Leiden 40: 305-319.
- Piercy, A. N., T. S. Ford, et al. (2006). Analysis of variability in vertebral morphology and growth ring counts in two Carcharhinid sharks. Environmental Biology of Fishes 77: 401-406.
- Pinheiro, J. C. and D. M. Bates (2000). Mixed-effects models in s and S-Plus. New York: Springer-Verlag.
- Pratt, H. L. J. (1979). Reproduction in the blue shark, *Prionace glauca*. Fish Bull. 77(445-469).
- Queiroz, N., N. Humphries, et al. (2010). Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. Mar Ecol Prog Ser 406: 265-270.
- QuinnII, T. J. and R. B. Deriso (1999). Quantitative Fish Dynamics. Oxford University Press, New York.
- Sanchez-Delta, J. A., C. Quinonez-Velazquez, et al. (2011). "Age and growth of the silky shark *Carcharhinus falciformis* from the west coast of Baja California Sur, Mexico." Journal of Applied Ichthyology 27 20-24.
- Silva, A. A., H. M. Silva, et al. (1996). " Some results on the biology of the blue shark, *Prionace glauca*, in the North Atlantic based on data from a research cruise of the R/V Arquipelago in Azorean waters: A summary paper."
- Silva, A. D., J. Hoey, et al. (2008). A historical index of abundance for the blue shark (*Prionace glauca*) in the western North Atlantic. Fisheries Research 92 (1): 41-52.
- Skomal, G. B. and L. J. Natanson (2003). Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Fishery Bulletin 101: 627-639
- Stevens, J. D. (1975). Vertebral rings as a mean of age determinations in the blue shark (*Prionace glauca* L.). Journal of Marine Biological Association of the United Kingdom 55(657-665).

- Stevens, J. D. (1976). First results of shark tagging in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom 56: 929-937.
- Stevens, J. D. (1984). Biological observations on sharks caught by sportfishermen off New South Wales. Aust. J. Mar. Freshwater Res. 35: 573-590.
- Suda, A. (1953). Ecological study of the blue shark (*Prionace glauca* Linné). South Sea Area Fish Research Laboratory Report 26: 1-11.
- Suda, A. (1953). Ecological study of the blue shark (*Prionace glauca* Linné'). South Sea Area Fisheries Research Laboratory Report 26: 1-11.
- Tanaka, S., G. M. Cailliet, et al. (1990). Differences in growth of the blue shark, *Prionace glauca*: technique or population. In Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries (Pratt, H. L., Gruber, S. H. & Taniuchi, T., eds). NOAA Technical Report NMFS 90: 177-188.
- Tanaka, S., G. M. Cailliet, et al. (1990). Differences in growth of the blue shark, *Prionace glauca*: technique or population? In: H.L. Pratt, Jr., S.H. Gruber, and T. Taniuchi (eds), Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and Status of the Fisheries. NOAA ech. Rep. 90: 177-187.
- Tucker, D. W. and C. T. Newnham (1957). The blue shark *Prionace glauca* breeds in British seas. Ann. Mag. Nat. Hist., Series 12 10: 673-688.
- Vigliola, L., M. L. Harmelin-Vivien, et al. (2000). Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of *Diplodus* from the Mediterranean sea. Canadian Journal of Fisheries and Aquatic Sciences 57: 1291-1299.
- Vigliola, L. and M. G. Meekan (2009). The back-calculation of fish growth from otoliths. Springer Science.
- Watson, J. T., T. E. Essington, et al. (2008). Trade-offs in the design of fishery closures: management of silky shark bycatch in the Eastern Pacific Ocean tuna fishery. Conserv. Biol. 23: 626-635.

Table 1. Von Bertalanffy growth parameters (SE) estimated by NLME for both studied shark species.

	<i>P. glauca</i>	log-Lik ratio	P	<i>C. falciformis</i>	log-Lik ratio	P
t_0	-0.89 (0.03)	-3863.4	0.10	-2.38 (0.06)	-422.4	0.43
K	0.161 (0.003)	-864.1	0.26	0.095 (0.006)	-422.9	0.21
L_∞	258 (3)	-3864.1	0.65	230 (9)	-422.4	0.23

Table II. Von Bertalanffy growth function (VBGF) parameters and back calculated parameters (BC) at maximum age derived from vertebral bands in blue shark and silky shark separated by geographic location and sex (Female F, Male M or sexes combined sex SC).

Authors	Location of studies	Sex	n	LF range (cm)	LF (cm) maturity	L_{∞} (cm)	K	t_0 (an)
BLUE SHARK								
Stevens (1975)	NE AO	SC	-	-	-	349	0.11	-1.04
Henderson et al. (2001)	NE AO	SC	159	55-191	184	314	0.12	-1.33
Skomal and Natanson (2003)	North AO	SC	411	49-312	183	285	0.17	-1.41
Silva et al. (1996)	NE Atlantic	SC	-	-	-	284	0.14	-1.08
Cailliet & Bedford (1983)	NE Pacific	SC	130	22-210	184	268	0.07	-3.75
Bianco-Parra et al. (2008)	CE Pacific	SC	204	68-226	156-178	303	0.10	-2.68
Skomal and Natanson (2003)	North AO	M	287	49-284	183	282	0.18	-1.35
Silva et al. (1996)	NE AO	M	-	-	-	309	0.12	-1.07
Cailliet & Bedford (1983)	NE PO	M	38	22-210	184	247	0.18	-1.11
Blanco-Parra et al. (2008)	NW AO	M	593	22-210	170	254	0.10	-2.44
Tanaka et al (1990)	NW PO	M	43	-	-	308	0.10	-1.38
Nakano (1994)	North PO	M	148	-	-	287	0.13	-0.76
Skomal and Natanson (2003)	North AO	F	119	49-312	183	310	0.13	-1.77
Silva et al. (1996)	NE AO	F	-	-	-	382	0.09	-1.19
Cailliet & Bedford (1983)	NE PO	F	88	-	184	203	0.25	-0.80
Blanco-Parra et al. (2008)	NW AO	F	324	76-211	156-178	200	0.15	-2.15
Tanaka et al (1990)	NW PO	F	152	-	-	254	0.16	-1.01
Nakano (1994)	North PO	F	123	-	-	243	0.14	-0.85
Lessa et al. (2004)	AO Brazil	SC	236	143-256	186-188	291	0.16	-1.01
Current study	SW IO	SC	188	36-276	150	255	0.16	-0.89
SILKY SHARK								
Joung et al. (2008)	NE Taiwan	SC	469	61-213	172-180	272	0.08	-2.76
Branstetter (1987)	Gulf Mexico	SC	135	72-223	176-188	243	0.15	-2.20
Oshitani et al. (2001)	PO	SC	298	27-284	140-156	168	0.15	-1.76
Joung et al. (2008)	NE Taiwan	M	256	66-213	174	258	0.10	-2.32
Joung et al. (2008)	NE Taiwan	F	213	61-196	172-180	280	0.07	-3.03
Oshitani et al. (2001)	PO	M	145	27-284	140-145	224	0.15	-1.76
Oshitani et al. (2001)	PO	F	153	27-284	150-156	224	0.16	-1.77
Sanchez-de Ita et al. (2011)	East PO	SC	252	74-218	151	201	0.14	-2.98
Current study	SW IO	SC	197	51-264	144	230	0.09	-2.38

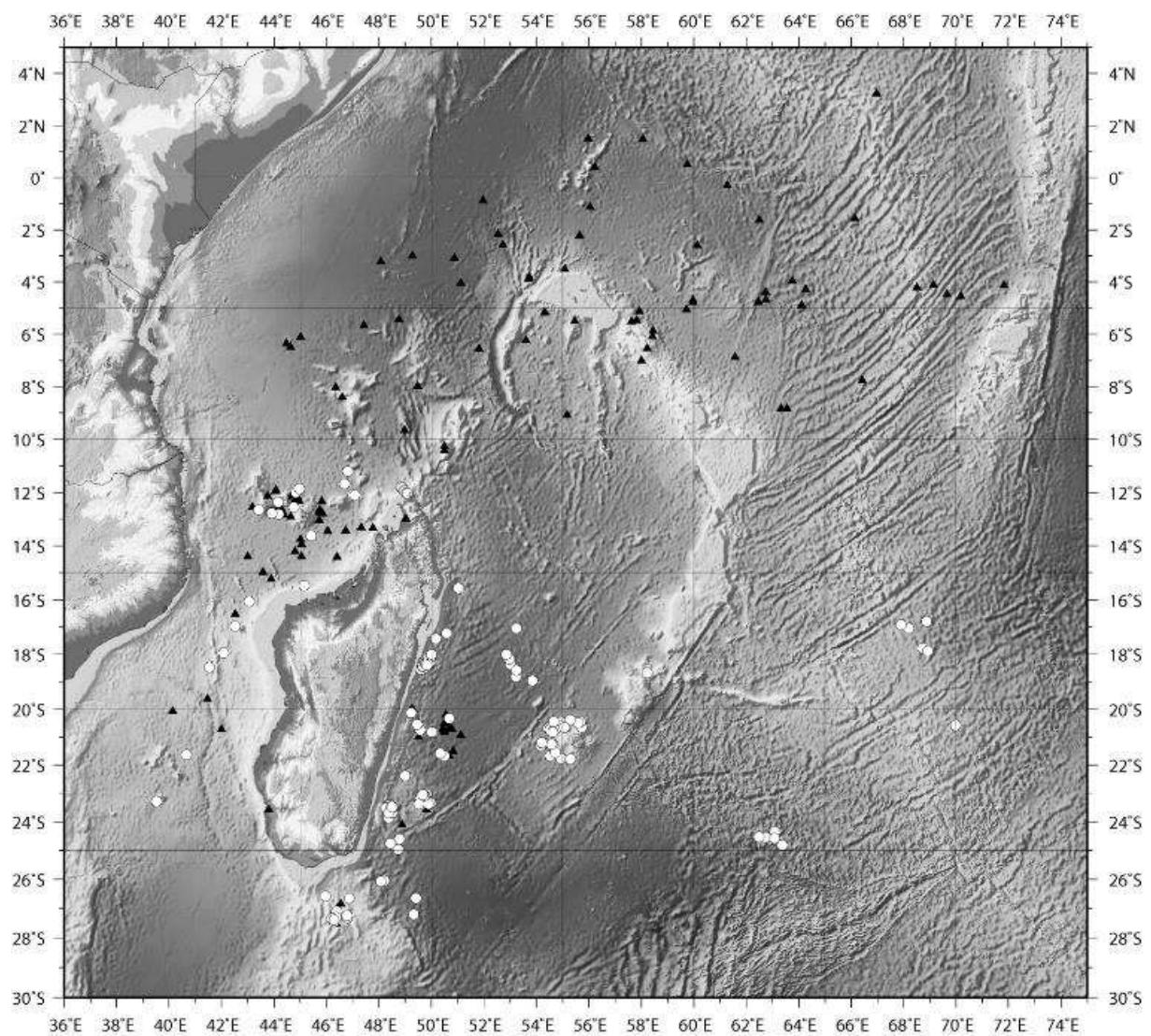


Figure 1. Sampling locations for *Prionace glauca* (white circle) and *Carcharhinus falciformis* (black triangle) in the Southwest Indian Ocean

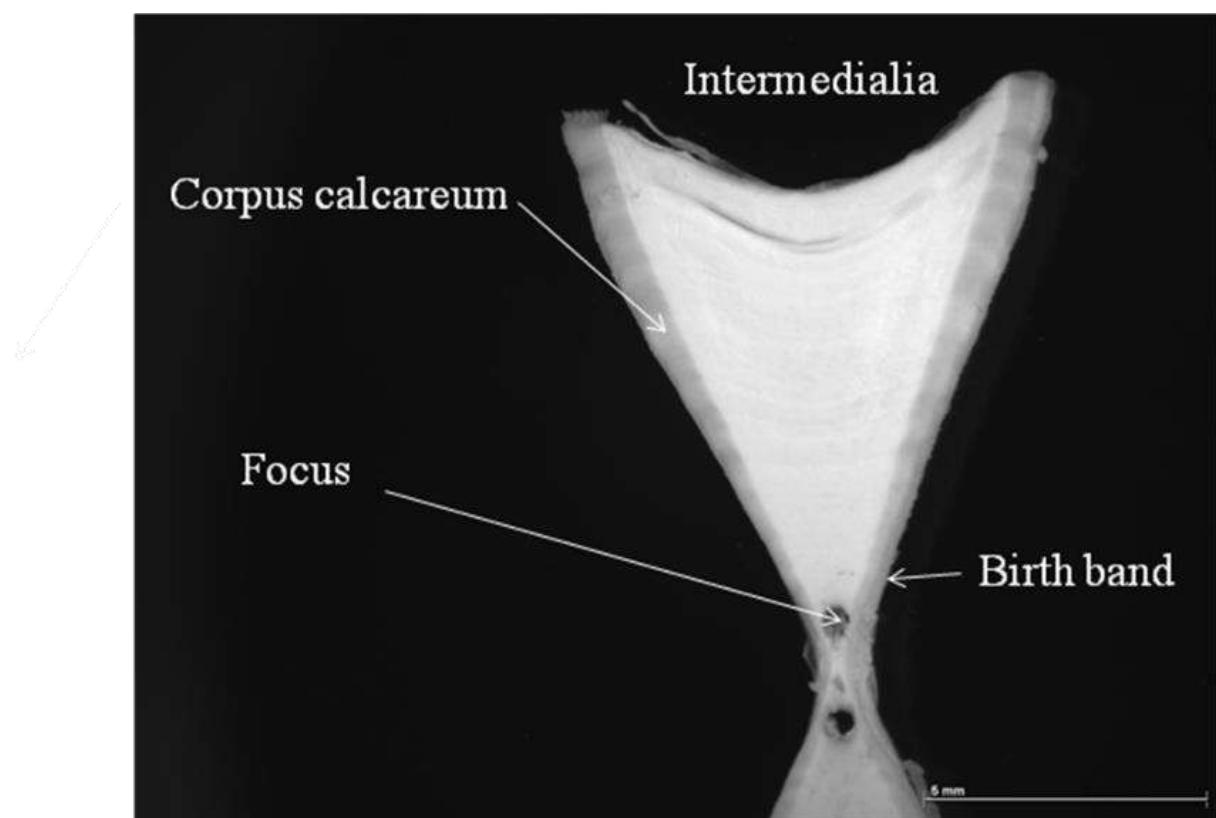


Figure 2. Cross section of a vertebra illustrating locations of the focus, corpus calcareum and birth band on a half bow-tie section – scale bar is 5mm

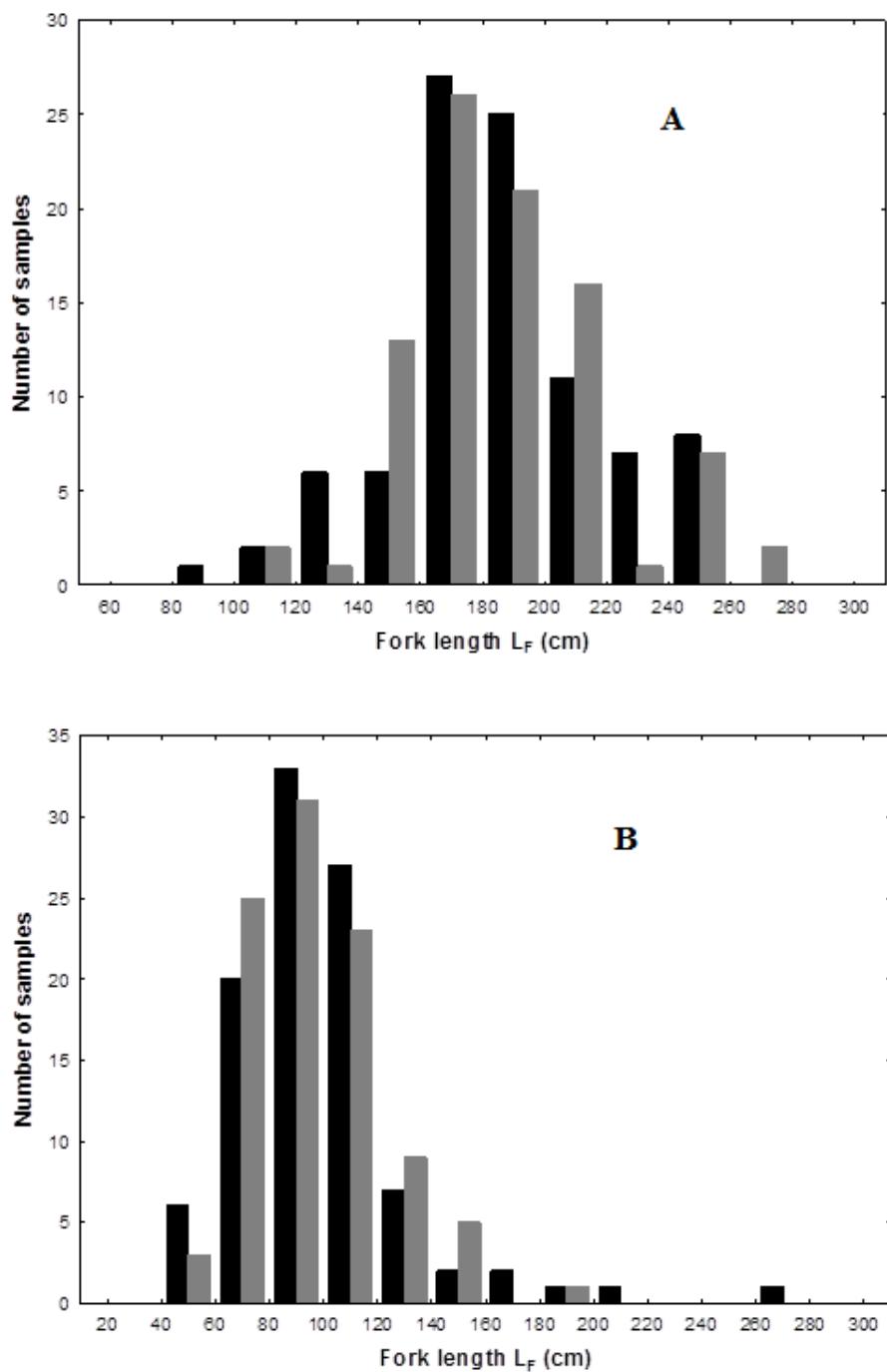


Figure 3: Frequency distribution of the fork length (cm) of female (black bar) and male (grey bar) for the blue shark (A) and the silky shark (B).

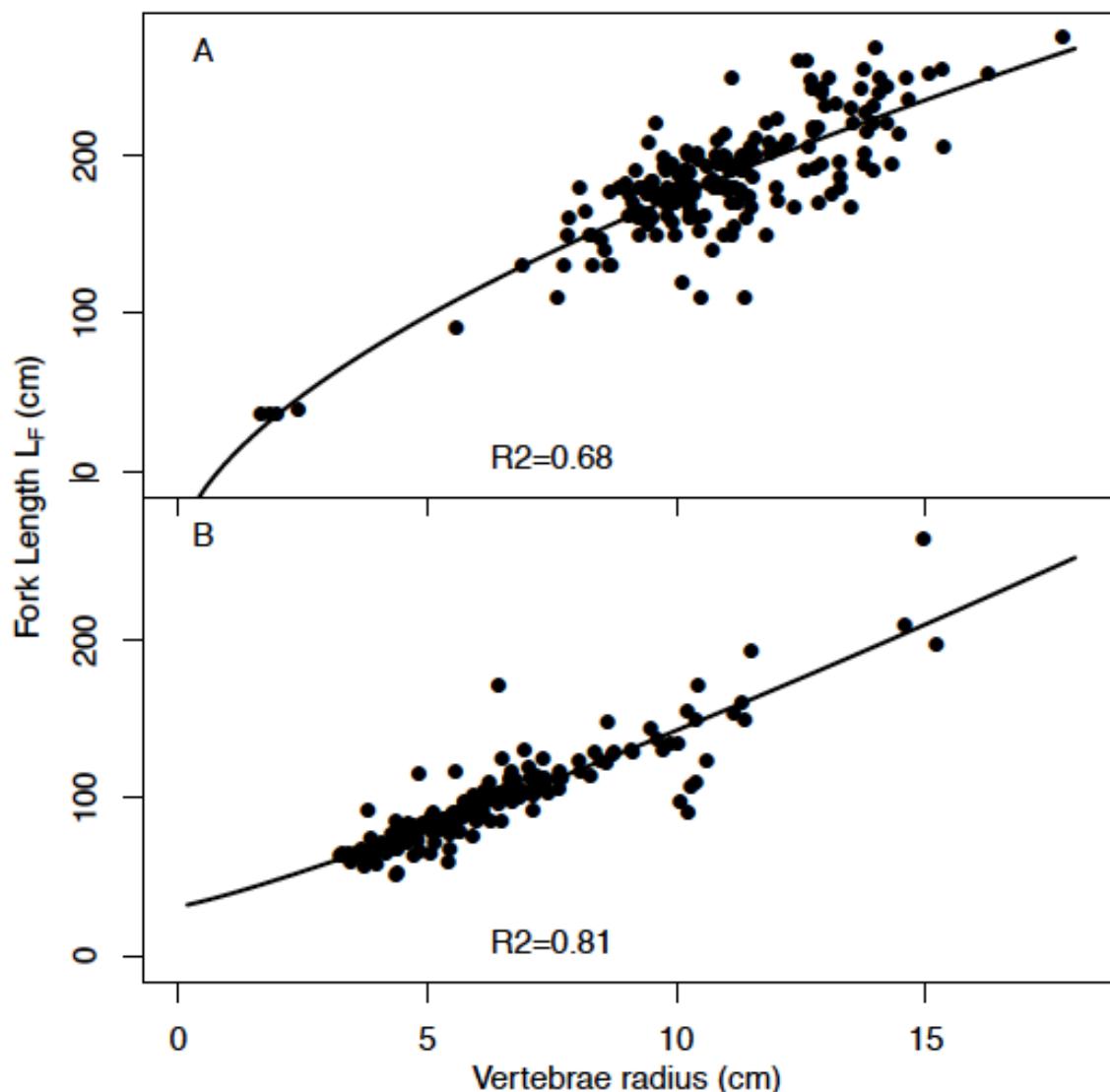


Figure 4: Relationship between the fish length (L) and the radius (R) of its vertebrae radius for the blue shark (A) and the silky shark (B). The solid line represents the least-square regression of the allometric L-R model.

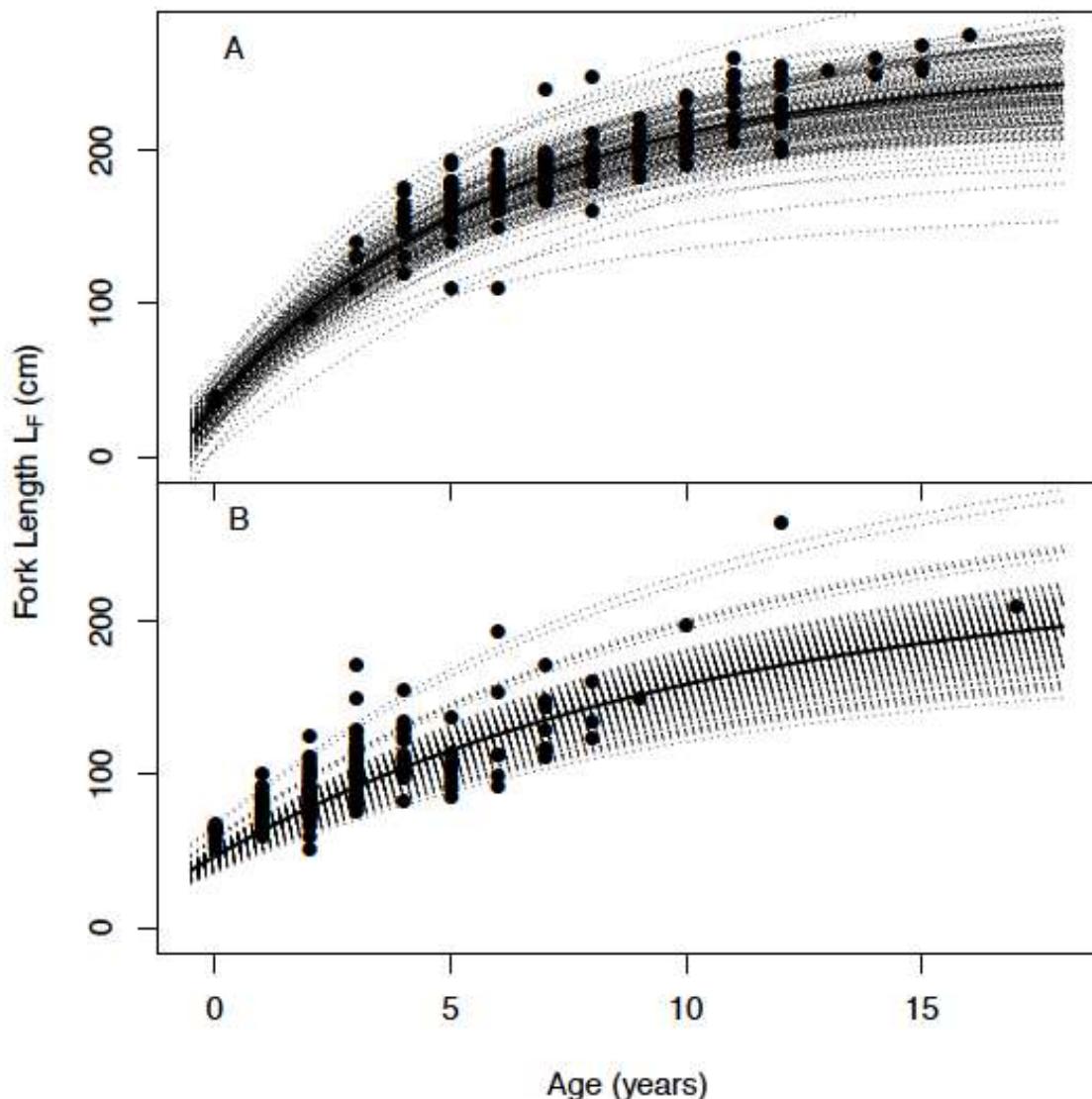


Figure 5. Back-calculated size-at-age data (modified Fry's model) and NLME fit of the von Bertalanffy growth equation for blue shark (A) and silky shark (B). Continuous lines represent population growth trajectories (fixed effects of the NLME), and dot-lines represent individual growth trajectories (mixed effects = fixed + random effects of the NLME).